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October 24, 1975

Professor L. L. Cavalli-Sforza
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Dear Luca:

It was a pleasure that I could see you (rather unexpectedly) in my recent visit to the United States. Many thanks to you for your hospitality then.

I have read your new manuscript "The Theory of Continuous Variation: A Direct Approach Through the Joint Distribution of Genotypes and Phenotypes" a copy of which you gave me at that time.

I think that it is an interesting and original contribution. Although I have not checked the details of your calculations I have little doubt that they are correct. I am very happy that one of my previous papers turned out to be of some use to you. Incidentally, I note that you are right in saying that $S = K/2$ (at the bottom of page 8) should read $S = 1/(2K)$.

Probably the most unexpected result in your paper is the demonstration that the heritability after selection can be greater than unity.

Since I thought that a great deal of selective elimination would be required to realize it, I made a few calculations to check this point. If I understand your paper correctly, the mean fitness is (assuming that the mean and the optimum coincide, i. e. $\bar{f} = \mu$);

$$\bar{W} = \int_{-\infty}^{\infty} \frac{1}{\sqrt{2\pi} \sqrt{E}} e^{-(f-\mu)^2/2E} \cdot e^{-(f-\mu)^2/2S} df$$

$$\therefore \bar{W} = \sqrt{\frac{S}{E + S}}$$

Noting that $W_{\text{optimum}} = W(\mu) = 1$, the amount of selective elimination is

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$$L = \frac{w_{op} - \bar{w}}{w_{op}} = 1 - \sqrt{S/(E + S)}$$

which is the load due to the centripetal selection involved.
Thus

$$S = \frac{(1 - L)^2}{1 - (1 - L)^2} \cdot E.$$

Substituting this into your condition $S^2 < M(E + 2S)$ on page 8, we get

$$\frac{E}{M} < \frac{1 - (1 - L)^4}{(1 - L)^4}$$

as a condition for the after-selection-heritability to be larger than unity.

The left hand side is the total phenotypic variance divided by the amount of variance added each generation by mutation. For example, if this is 99, L turns out to be larger than 0.68, or 68% mortality. This seems to me an intense selection for a human population.

I do not know whether the above point is of any interest to you, but I am communicating it any way to show that I studied your paper.

With best wishes to you as always. Please convey my kind regards to Alba, and also to Jim McGregor.

Sincerely,



Motoo Kimura

MK/ym